Consequences of Earthworms in Agricultural Soils: Aggregation and Porosity

7

W.M. Edwards and M.J. Shipitalo

Soil Scientists, USDA-ARS, at the North Appalachian Experimental Watershed, Coshocton, OH 43812-0488

n agricultural ecosystems, the soil serves as the framework for the physical, chemical, and biological processes that make conditions suitable for crop production. We manage soil properties and processes with tillage, irrigation, drainage, nutrients, and pesticides to increase profitability and to protect long-term productivity and the local environment.

Within the wide range of soils and climates, farmers use many management options to influence such measurable soil properties as density, aggregation, pore size distribution, water and organic matter contents, chemical distributions, and the rate that chemical transformations take place. In trying to make field soils more favorable for crop production, we often inadvertently make the managed soil more or less favorable for soil invertebrates. Therefore, the resulting agronomic responses to management may be due partially to unmeasured changes in populations and activity of many different soil organisms.

Earthworms, because of their size, abundance, and activity, can make visible and easily measured changes in soil properties. In high numbers, earthworms can have notable effects on soil structure and porosity. Therefore, we must consider not only the direct effects of management on soil properties and processes, but also their effects on earthworm populations.

AGGREGATION

Soil structure and the consequences of its variation are hard to quantify. Although many physical and chemical factors that influence soil structure have been documented (Allison 1968; Greenland 1981; Hamblin and Davies 1977; McKeague et al. 1987; Oades 1984, 1993), it is difficult to relate improvements in aggregation or aggregate stability to enhanced crop growth. Similarly, Logsdon and Linden (1992) noted that few reliable field studies have documented improved root and plant growth due to the effects of earthworms on soil structure.

Especially in humid regions, earthworms and other soil fauna usually have positive effects on soils (Dindal 1985; Edwards and Lofty 1977; Hole 1981; Lee 1985; Lee and Foster 1991). Shaw and Pawluk (1986), however, noted that earthworms can also have negative effects on soil physical condition, depending on the species of earthworms and/or the nature of the soil.

Although earthworms generally increase the size and stability of aggregates, primarily in the uppermost soil horizons, exceptions have been reported (Hopp and Hopkins 1946; MacKay and Kladivko 1985; Blanchart et al. 1989; Brussaard et al. 1990). Kladivko et al. (1986) showed that *Lumbricus rubellus* (Hoff.) increased both the mean weight diameter and stability of aggregates which had a favorable effect on reducing crusting and enhancing crop emergence. Hamilton and Dindal (1989) noted that one species, *Lumbricus terrestris* (L), improved aggregation in sludge-amended plots whereas another species, *Eisenia fetida* (Sav.), had no effect. This is not surprising since *E. fetida* is not a soil species.

The stability of fresh earthworm casts, which eventually become components of soil structure, can vary tremendously depending upon moisture status and age (Shipitalo and Protz 1988; Marinissen and Dexter 1990) and the earthworm's diet (Shipitalo et al. 1988). Shaw and Pawluk (1986) found that the production of more desirable soil fabrics made by earthworms was correlated with increased concentrations of a clay-bound carbohydrate. The proliferation of fungal hyphae on the surface has also been related to increased stabilization of casts with age (Marinissen and Dexter 1990).

At the microfabric scale, earthworms affect soils by thoroughly mixing organic and mineral components as they are passed through the earthworm gut. In this process the existing soil structure is destroyed, and some organic components are liberated while others may be protected by the formation of new casts and aggregates (Shipitalo and Protz 1988, 1989; Barois et al. 1993).

Characteristics of the resultant casts, whether deposited on the surface or below, vary among earthworm species and are affected by soil and vegetation factors (Tomlin et al. 1995). The most compact casts of the tropical geophagous earthworm, *Millsonia anomala* (Omodeo), are so dense that carbon mineralization in the casts is reduced compared to that in sieved soil (Martin 1991). The

slower movement of air and water in these casts inhibits biochemical reactions (Blanchart et al. 1993), effectively blocking mineralization for months and even years in the compact structure of aged casts (Lavelle and Martin 1992). In a cold, Canadian soil, fecal pellets of earthworms were so dense that the smaller units within were strongly fused and their structural integrity was frequently lost (Juma 1991). Altemüller and Joschko (1992) developed a fluorescent staining technique that aided identification and diagnostic interpretation of earthworm casts in complex cast/aggregate mixtures. Martin and Marinissen (1993) more thoroughly discussed effects of earthworms on processes that influence stability, nutrient release, and decomposition of faunal excrements.

It is not surprising that science has not clearly defined all of the effects of earthworms on soil structure. There is general agreement, however, that most earthworms burrow, cast, and mix mineral and organic components of the soil, and high earthworm numbers have more effect on soil properties than sparse populations. Blanchart (1992) directly assessed earthworm effects on restructuring of a Savanna soil by measuring the aggregate distribution of undisturbed soil columns by sieving the material before replacing it in the field without invertebrates, with native soil invertebrates, or with added earthworms (*M. anomala*). Thirty months later the columns were excavated again. The proportion of >2.0-mm aggregates was nearly four times greater with native soil fauna and nearly five times greater with *M. anomala* than in the soil without any fauna.

As was reported by Tomlin et al. (1995), the organic component of the earthworms' diet may be as much as 25 Mg/ha/yr of cow dung (Guild 1955) or 3 Mg/ha of deciduous leaf fall in approximately three months (Satchell 1967). Where a limited supply of palatable organic matter or harsh soil surface conditions limited earthworm activity, the addition of manure consistently increased earthworm numbers (Berry and Karlen 1993). As food supply limits populations, it also controls cast production which can range from almost nil to >2,500 Mg/ha/yr in the tropics (Watanabe and Ruaysoongnern 1984).

In temperate climates, where most earthworm activity is concentrated in the spring and autumn months, the stability of casts and their conversion into stable aggregates may depend on when they are produced. The vegetation supply will differ between spring and autumn, and the weather conditions following casting, which influence drying, may differ greatly. Even within the spring or autumn casting periods, the fate of a surface or near-surface cast will be very different if it is produced immediately before a 5-cm rain storm or a two-week drought. Similarly, in the tropics where casting rates are commonly high (Lee 1985; Lavelle et al. 1989), the stability of casts produced at the beginning of a rainy season and their subsequent contribution to soil aggregation may be quite different from those produced at the beginning of the dry season.

In addition to the physical, temporal, climatic, and species differential effects on earthworm casts and aggregation, measurement strategies also add to variability. Worms interact with many other soil organisms, and measuring the effects of only part of the complex mixture often results in less than perfect understanding of the direct and indirect causes of the observed results.

Research on factors affecting the stability of earthworm casts has been reviewed thoroughly by Oades (1993) and Tomlin et al. (1995). The physical nature of casts has a major influence on organic matter and nitrogen transformations (Tisdall and Oades 1982; Van Veen and Kuikman 1990). Further evidence of the complexity of earthworm effects on soil structure was presented by Hamilton et al. (1988), who studied earthworm interactions in soil microcosms that had received sludge amendments, and by Hartenstein (1986), who reviewed and interpreted global earthworm biotechnology.

POROSITY AND INFILTRATION

Field Studies

The activity of most burrowing soil organisms tends to increase soil porosity, pore size, and the variability of porosity. These changes affect many soil processes. For instance, Knight et al. (1992) showed that earthworms increased soil macroporosity and tripled the amount of leaching from pastures in England. Because of the continuity of many biopores, especially earthworm burrows (Bouché 1971; Edwards et al. 1988b; Schrader 1993), a single biopore can dominate water movement under some conditions as measured by traditional soil physical methods. Smettem and Collis-George (1985b) showed that a single, continuous 0.3-mm-diameter macropore can conduct more water than the rest of a 100-mm-diameter soil sample.

L. terrestris burrows are easily recognized, vertically continuous biopores that have been implicated in "short-circuiting" water and solutes in soils (Bouma et al. 1981; Steenhuis et al. 1990; Wildenschild et al. 1994). This phenomenon is also termed "by-pass flow" and can be characterized by early breakthrough of chemical tracers (Bouma et al. 1983; Bouma 1991). Colored dyes and other tracers have been used by numerous investigators to confirm that flow can occur in these burrows and other preferential flow paths (Ehlers 1975; Linden and Dixon 1976; Douglas et al. 1980; Bouma 1981; Tyler and Thomas 1981; Germann et al. 1984; Smettem and Collis-George 1985a; Smith et al. 1985; Zachmann et al. 1987; Everts et al. 1989; Andreini and Steenhuis 1990).

Lee (1985) and Smettem (1992) reviewed research documenting high infiltration rates in soils containing earthworms (Hopp and Slater 1948; Teotia et al.

1950; Scharpenseel and Gewehr 1960; Stockdill 1966; Carter et al. 1982) and into individual earthworm burrows (Ehlers 1975) or burrow systems (Bouché 1971). Just as the introduction of earthworms has been shown to increase infiltration (Stockdill 1966; Kladivko et al. 1986; Joschko et al. 1992), the elimination of earthworms by repeated insecticide applications has reduced infiltration rates (Clements 1982; Sharpley et al. 1979).

Urbánek and Dolezal (1992) surveyed the abundance and hydraulic efficiency of earthworm channels in Czechoslovakian soils and reported that burrows can increase infiltration and speed drainage to the deep tile level. However, Ela et al. (1992) concluded from pot experiments using soils from the northern Corn Belt of the United States that the addition of *Aporrectodea tuberculata* did not increase simulated rainfall infiltration. Their burrows did not go deep into the soil, and the soil surface quickly sealed any openings to the burrows. It may be that *L. terrestris* contribute to surface sealing or crusting by removing protective residue from parts of the soil surface as they create middens.

Two potentially important consequences of infiltration in earthworm burrows involve reduced surface runoff and the possibility for increased percolation through the soil profile. In most agricultural situations, reducing runoff and the overland transport of sediments and chemicals is desired. An unwanted increase of chemical movement through the root zone, however, may accompany increased infiltration (Zachmann et al. 1987; Isensee et al. 1990; Shipitalo et al. 1990; Steenhuis et al. 1990; Trojan and Linden 1992; Propes et al. 1993). In some parts of the eastern United States, where no-tillage has replaced conventional moldboard plowing of sloping fields for row-crop production, runoff and erosion have been greatly reduced while infiltration and populations of the vertically-burrowing *L. terrestris* have increased (Edwards 1991; Bohlen et al. 1995).

Because *L. terrestris* numbers usually increase under no-tillage and the lack of disruptive tillage allows old burrows to persist, the number of burrows per unit area can increase with years of continuous no-tillage production. With more water infiltrating into the non-tilled fields each year and with the increased number of *L. terrestris* burrows in these soils, the opportunity for preferential flow that bypasses the soil matrix increases. Additionally, annual chemical inputs required for continuous no-tillage row crop production may be much greater than those used previously when the crop rotation needed for erosion control included several years of meadow. Therefore, much of the recent hydrologic research in sloping, humid areas, where no-tillage is an important management practice, has involved identifying factors and conditions under which nutrients and herbicides used in row-crop production may move down in *L. terrestris* burrows.

In one study, the number of biopores >0.4 mm in diameter was determined at four depth intervals within the top 30 cm of a long-term no-till corn watershed

using image analyses of field photos (Edwards et al. 1988a). These silt loam surface horizons averaged >14,500 such pores per m^2 , 160 of which were L. terrestris burrows >5 mm in diameter. Mean pore diameter ranged between 1 and 2 mm, and the number of pores was inversely proportional to pore diameter. The >0.4-mm-diameter pores comprised <1.5 % of the area at four measured depths, but tracer studies showed that surface water could infiltrate rapidly through the larger pores, possibly contributing to a reduction in runoff from the gauged watershed (Germann et al. 1984).

Buried samplers were installed to intercept and characterize water infiltrating in *L. terrestris* burrows near gauged watersheds (Edwards et al. 1989) and in farmer-owned fields (Shipitalo et al. 1994). Water infiltrating through burrows averaged 4% of the rainfall in 12 summer storms that were big enough to cause burrow flow; however, burrow flow accounted for 10% of the rain in a brief, high-intensity storm that fell under very dry antecedent surface conditions. Both studies showed that downward movement of chemicals in the burrows was small, approximately 5% of the total NO₃-N, Br and Sr transport as determined from pan lysimeter measurements (Shipitalo et al. 1994).

Laboratory Studies

The field studies documented that water infiltrated frequently in *L. terrestris* burrows, as a result of natural storms falling on no-till fields. They also showed that rainfall intensity, antecedent soil moisture, and time between surface application of the chemicals and subsequent rainfall events influenced the concentration and downward transport of chemicals. Van Ommen et al. (1989) reached similar conclusions after studying infiltration with solutes and dye in field plots in the Netherlands.

Dependency on natural storms made field evaluation of specific factors that might affect chemical transport in burrow flow difficult. Therefore, a system was developed at the USDA hydrologic experiment station, Coshocton, Ohio, that enabled the drip-application of water at controlled intensity to the surface of 30-by-30-by-30-cm blocks of undisturbed soil collected from no-till fields (Shipitalo et al. 1990). The location of ≥2.0-mm-diameter biopores at the bottom surface of each block was recorded with respect to a 64-compartment grid that supported the block under a rainfall simulator. During each simulated storm, water infiltrated through each of the 64 grid cells could be measured, sampled, and related to macroporosity in individual cells.

Shipitalo et al. (1990) used this simulator to show that if a small, low-intensity storm fell on a residue-covered surface shortly after atrazine application, concentration and transport of the herbicide in *L. terrestris* burrows in a subsequent average-sized storm was half as great as when the average storm

occurred without the preceding small one. The small simulated storm caused no flow through the test blocks, but by wetting and possibly leaching herbicide from the residue into the surface soil, it effectively reduced transport of herbicides in burrow flow in subsequent storms. Repeated storms on the same soil blocks that did not receive additional herbicide treatments showed that the concentration of atrazine in burrow flow decreased in successive events, regardless of intensity and amount of water in preceding storms. Propes et al. (1993) also reported that a low-volume pretreatment storm caused more atrazine to be retained by the soil matrix as compared to samples that did not receive the pretreatment storm.

The results of the study by Shipitalo et al. (1990) also indicated that near-surface water content also affected chemical flow in the burrows. As noted by Germann et al. (1984), White (1985), and Edwards et al. (1989), the residue-covered surface of nontilled soil appears to be somewhat hydrophobic under dry antecedent conditions, limiting infiltration into the soil matrix for a few minutes at the onset of storms. Chan (1992) investigated this condition and attributed the initial water repellency at the surface of direct drilled fields to the growth of fungal hyphae under slow drying conditions, the absence of soil disturbance, and the presence of a permanent layer of organic matter. Bisdom et al. (1993) concluded that water repellency of sandy soils was caused by organic components in micro-aggregates, plant fragments, and coatings on sand grains and could be influenced by soil biota such as earthworms. Bond (1969) reviewed several factors that influence water repellency of soils and its potential effect on infiltration.

The rainfall simulator in Ohio was used in a subsequent study to evaluate the effect of storm intensity on the movement of water and herbicides in earthworm burrows. Relatively dry blocks (15% v/v), partially covered with corn residue from previous crops, received 30 mm of simulated rain at intensities of 120, 60, or 15 mm/hr (Edwards et al. 1992a). The results supported the conclusions from the field studies that more of the *L. terrestris* burrows produced flow and more of the applied water passed through burrows in the blocks as storm intensity increased. Although the concentration of surface-applied atrazine in the burrow flow was not affected by rainfall intensity, total transport of atrazine in burrow flow increased with intensity because the volume of burrow flow increased. Trojan and Linden (1992) reported that burrows of *A. tuberculata* also transported more water when subjected to higher simulated rainfall intensities.

The block studies of Edwards et al. (1992a) also showed that the dry surface of the blocks allowed water to enter the *L. terrestris* burrows soon after the onset of rainfall and run through the 30-cm-deep blocks almost immediately. At the 120-mm/hr intensity, free water dripped out of some burrows within two minutes of the rainfall start, after <4.5 mm of water had been applied to the surface.

At lower application intensities, flow through the blocks began later and fewer of the burrows were involved in the rapid transport of water.

Field watershed and plot studies have shown that the first storm following surface application of chemicals, especially if it occurs soon after application, usually contains the highest concentrations of those chemicals in surface runoff water (Baker and Laflen 1983; Owens et al. 1984). To determine if time between pesticide application and the onset of the first subsequent storm had a similar effect on chemical transport in subsurface flow, three blocks received a simulated storm either one hour, one day, one week, two weeks, or six weeks after atrazine was applied to the residue-covered surface (Edwards et al. 1993). No rain fell on the blocks during the first two weeks of the experiment, other than the 30-mm simulated storms. Transport of atrazine in burrow flow, through the blocks that received the storm one hour after herbicide application, was three times greater than that through the blocks that received similar storms two weeks later. Four small natural storms fell on the final three blocks before they were brought in from the field to the simulator. Due to the extra time following chemical application, and to the four small storms that preceded the simulated rain, transport of atrazine in burrow flow on the six-week blocks averaged 2% of that from the blocks treated one hour before the simulated storm (Edwards et al. 1993).

The observed flow in *L. terrestris* burrows at 30 cm depth, as early as two minutes after the onset of rain, indicates that the entry of water into the burrows must take place very near the soil surface. It also indicates that the water that drains freely from burrows at the bottom of the blocks soon after the onset of rain could not have infiltrated into the fine pore matrix of the soil where it would be held under high tension. Therefore, the first water to accumulate in depressions on the soil surface may pick up atrazine, which was sprayed on the surface, and transport it down in the earthworm burrows without interaction with the antecedent soil water.

We evaluated the range of likely concentrations of atrazine that would be available to infiltrate in earthworm burrows in treated fields (Edwards et al. 1996). One day after atrazine was sprayed on the surface of corn fields, we used syringes to collect 10-mL samples of the first water to accumulate in small surface depressions after onset of simulated rainfall. With continued application of water from the simulator, subsequent samples of water from the same depression were collected at 5-minute intervals for 30 minutes. The experiment consisted of five replications of this sampling sequence on days 1, 2, 4, 8, 16, and 32 following herbicide application on three corn fields: no-till with manure, no-till without manure, and moldboard plowing without manure. The simulator was moved to a new location in each field for each sampling.

In every case, the concentration of atrazine was highest in the first sample collected from a depression and was from 50 to 90% lower in water from that depression 30 minutes later. The first samples from the plowed field contained atrazine concentrations as much as 200% higher than those from the mulch-covered fields. The pattern of decreasing atrazine concentration during the 30-minute simulated rain continued through all sampling days with the final concentrations on day 32 being approximately 1% of the initial concentrations on day 1.

Burrow Linings

Chemical transport through earthworm burrows may differ from that through similar size macropores of non-biological origin (Turner and Steele 1988; Trojan and Linden 1992). The species *L. terrestris* casts within its burrow so that the lining, or drilosphere, is rich in organic matter, microorganisms, and available plant nutrients, providing a channel ideal for root growth (Edwards and Lofty 1980; Pawluk and Bal 1985; Mouat and Keogh 1987). Mucus secreted through the earthworm's cuticle and often noted on burrow walls has been shown to neutralize the pH of the drilosphere, by either raising or lowering pH when the surrounding conditions are too acid or alkaline, respectively (Schrader 1991, 1993).

Edwards et al. (1992b) poured herbicide-laden water into *L. terrestris* burrows and found much lower concentrations in the water intercepted 50 cm below, only seconds later. Stehouwer et al. (1993, 1994) investigated the characteristics of burrow linings at several depths as compared to those of the surrounding bulk soil. They showed that *L. terrestris* burrow linings were enriched in organic C, relative to the soil matrix, and that the C enrichment was correlated with enhanced sorption of atrazine on the burrow linings (Stehouwer et al. 1993). They also poured water containing several herbicides through *L. terrestris* burrows and similar-sized man-made holes in blocks of no-till soil. Sorption of the more strongly sorbed herbicides was enhanced by a factor of three on the burrow lining, relative to the bulk soil, while there was little difference in retention of two weakly sorbed herbicides as they passed through both the burrows and the man-made holes (Stehouwer et al. 1994).

SUMMARY

Numerous studies have been conducted to quantify the effects of earthworms on soil aggregation and porosity of agricultural soils. Most results indicate that

earthworms, through their burrowing activities and their search for food, can ingest large quantities of soil and organic matter. Passage of this material through the earthworm gut disrupts preexisting aggregates, but results in the intimate mixing of mineral and organic matter. Reformation of stable aggregates in the casted material depends on a number of factors, including the nature and relative amounts of mineral and organic matter ingested, where and when casts are deposited, and species of earthworm.

The burrows formed by earthworms can serve as preferential pathways for root growth, water movement, and chemical transport. Continuity and persistence of burrows are influenced directly by tillage practices. Entry of water and chemicals into the earthworm-formed macropores is dependent on weather-related factors (such as rainfall amount, intensity, and timing), soil moisture content, chemical characteristics, and method of application.

Despite much research, answers to some fundamental questions remain elusive. We still do not know how important earthworm activity is to maintaining aggregation and productivity of agroecosystems in general. Likewise, the conditions under which chemical transport through earthworm burrows ultimately affects groundwater contamination are still uncertain.

REFERENCES CITED

- Allison, F.E. 1968. Soil aggregation—Some facts and fallacies as seen by a microbiologist. Soil Sci. 106:136–143.
- Altemüller, H.J., and M. Joschko. 1992. Fluorescent staining of earthworm casts for thin section microscopy. Soil Biol. Biochem. 24:1577–1582.
- Andreini, M.S., and T.S. Steenhuis. 1990. Preferential paths of flow under conventional and conservation tillage. Geoderma 46:85–102.
- Baker, J.L., and J.M. Laflen. 1983. Water quality consequences of conservation tillage. J. Soil Water Conserv. 38:186–193.
- Barois, I., G. Villemin, P. Lavelle, and F. Toutain. 1993. Transformation of the soil structure through *Pontoscolex corethrurus* (Oligochaeta) intestinal tract. Geoderma 56:57–66.
- Berry, E.C., and D.L. Karlen. 1993. Comparison of alternative farming systems. II. Earthworm population density and species diversity. Amer. J. Alt. Agric. 8:21-26.
- Bisdom, E.B.A., L.W. Dekker, and J.F.Th. Schoute. 1993. Water repellency of sieve fractions from sandy soils and relationships with organic material and soil structure. Geoderma 56:105-118.
- Blanchart, E. 1992. Restoration by earthworms (Megascolecidae) of the macroaggregate structure of a destructured savanna soil under field conditions. Soil Biol. Biochem. 24: 1587–1594.
- Blanchart, E., P. Lavelle, and A.V. Spain. 1989. Effects of two species of tropical earthworms (Oligochaeta: Eudrilidae) on the size of aggregates in an African soil. Revue d'Ecologie et de Biologie du Sol 26:417–425.

- Blanchart E., A. Bruand, and P. Lavelle. 1993. The physical structure of casts of *Millsonia anomala* (Oligochaeta: Megascolecidae) in shrub savanna soil (Côte d'Ivoire). Geoderma 56:119–132.
- Bohlen, P.J., W.M. Edwards, and C.A. Edwards. 1995. Earthworm community structure and diversity in experimental agricultural watersheds in northeastern Ohio. Plant Soil 170: 233–239.
- Bond, R.D. 1969. Factors responsible for water repellence of soils. pp. 259–264. In L.F. De Bano and J. Letey (eds.). Proc. Symp. on Water Repellent Soils. University of California, Riverside.
- Bouché, M.B. 1971. Relations entre les structures spatiales et fonctionelles des écosystemes, illustrées par le rôle pédobiologique des vers de terre. pp. 189–209. In C. Delamere Deboutteville (ed.). La Vie dans les Sols. Gauthiers Villars, Paris.
- Bouma, J. 1981. Soil morphology and preferential flow along macropores. Agric. Water Mgt. 3:235–250.
- Bouma, J. 1991. Influence of soil macroporosity on environmental quality. Advances in Agronomy, 46. Academic Press, San Diego, CA, pp. 1–37.
- Bouma, J., C. Belmans, L.W. Dekker, and W.J.M. Jeurissen. 1983. Assessing the suitability of soils with macropores for subsurface liquid waste disposal. J. Environ. Qual. 12: 305–311.
- Bouma, J., L.W. Dekker, and C.J. Muilwijk. 1981. A field method for measuring short-circuiting in clay soils. J. Hydrol. 52:347–354.
- Brussaard, L., D.C. Coleman, D.A. Crossley, Jr., W.A.M. Didden, P.F. Hendrix, and J.C.Y. Marinissen. 1990. Impacts of earthworms on soil aggregate stability. Transactions of the 14th International Congress of Soil Science, Kyoto, Japan, III:100–105.
- Carter, A., J. Heinonen, and J. de Vries. 1982. Earthworms and water movement. Pedobiologia 23:395–397.
- Chan, K.Y. 1992. Development of seasonal water repellence under direct drilling. Soil Sci. Soc. Am. J. 56:326–329.
- Clements, R.O. 1982. Some consequences of large and frequent pesticide applications to grassland. pp. 393–396. In K.E. Lee (ed.). Proc. 3rd Australasian Conf. Grass. Invert. Ecol. S. Aust. Gov. Printer, Adelaide.
- Dindal, D.L. 1985. Soil animals and soil fabric production: Facts and perceptions. Quaestiones Entomologicae 12:587–594.
- Douglas, J.T., J.J. Gross, and D. Hill. 1980. Measurements of pore characteristics in a clay soil under ploughing and direct drilling, including the use of a radioactive tracer (144Ce) technique. Soil Tillage Res. 1:11–18.
- Edwards, C.A., and J.R. Lofty. 1977. Biology of Earthworms. Chapman and Hall, London, England. 333 pp.
- Edwards, C.A., and J.R. Lofty. 1980. Effects of earthworm inoculation upon the root growth of direct drilled cereals. J. Appl. Ecol. 17:533–543.
- Edwards, W.M. 1991. Soil structure: Processes and management. pp. 7–14. In R. Lal and F.J. Pierce (eds.). Soil Management for Sustainability. Soil and Water Conservation Society, Ankeny, IA.
- Edwards, W.M., L.D. Norton, and C.E. Redmond. 1988a. Characterizing macropores that affect infiltration into non-tilled soil. Soil Sci. Soc. Am. J. 52:483–487.
- Edwards, W.M., M.J. Shipitalo, and L.D. Norton. 1988b. Contribution of macroporosity to

- infiltration into a continuous corn no-tilled watershed: Implications for contaminant movement. J. Contamin. Hydrol. 3:193-205.
- Edwards, W.M., M.J. Shipitalo, L.B. Owens, and L.D. Norton. 1989. Water and nitrate movement in earthworm burrows within long-term no-till cornfields. J. Soil Water Conserv, 44:240–243.
- Edwards, W.M., M.J. Shipitalo, W.A. Dick, and L.B. Owens. 1992a. Rainfall intensity affects transport of water and chemicals through macropores in no-till soil. Soil Sci. Soc. Am. J. 56:52–58.
- Edwards, W.M., M.J. Shipitalo, S.J. Traina, C.A. Edwards, and L.B. Owens. 1992b. Role of Lumbricus terrestris (L.) burrows on quality of infiltrating water. Soil Biol. Biochem. 24:1555–1561.
- Edwards, W.M., M.J. Shipitalo, L.B. Owens, and W.A. Dick. 1993. Factors affecting preferential flow of water and atrazine through earthworm burrows under continuous no-till corn. J. Environ. Qual. 22:453–457.
- Edwards, W.M., M.J. Shipitalo, R. Lal, and L.B. Owens. 1996. Rapid changes in concentration of herbicides in corn field surface depressions. J. Soil Water Conserv. (in press).
- Ehlers, W. 1975. Observations on earthworm channels and infiltration on tilled and untilled loess soil. Soil Sci. 119:242–249.
- Ela, S.D., S.C. Gupta, and W.J. Rawls. 1992. Macropore and surface seal interactions affecting water infiltration into soil. Soil Sci. Soc. Am. J. 56:714–721.
- Everts, C.J., R.S. Kanwar, E.C. Alexander, Jr., and S.C. Alexander. 1989. Comparison of tracer mobilities under laboratory and field conditions. J. Environ. Qual. 18:491–498.
- Germann, P.F., W.M. Edwards, and L.B. Owens. 1984. Profiles of bromide and increased soil moisture after infiltration into soils with macropores. Soil Sci. Soc. Am. J. 48:237–244.
- Greenland, D.J. 1981. Soil management and soil degradation. J. Soil Sci. 32:301-322.
- Guild, W.J.McL. 1955. Earthworms and soil structure. pp. 83–98. In D.K.McE. Kevan (ed.). Soil Zoology. Butterworths, London.
- Hamblin, A.P., and D.B. Davies. 1977. Influence of organic matter on the physical properties of some East Anglian soils of high silt content. J. Soil Sci. 28:11–22.
- Hamilton, W.E., and D.L. Dindal. 1989. Impact of landspread sewage sludge and earthworm introduction on established earthworms and soil structure. Biol. Fert. Soils 8:160–165.
- Hamilton, W.E., D.L. Dindal, D.M. Parkinson, and J.J. Mitchell. 1988. Interaction of earthworm species in sewage sludge-amended soil microcosms: *Lumbricus terrestris* and *Eisenia fetida*. J. Appl. Ecol. 25:847–852.
- Hartenstein, R. 1986. Earthworm biotechnology and global biogeochemistry. Adv. Ecol. Res. 15:379–409.
- Hole, F.D. 1981. Effects of animals on soil. Geoderma 25:75-112.
- Hopp, H., and H.T. Hopkins. 1946. Earthworms as a factor in the formation of water-stable aggregates. J. Soil Water Conserv. 1:11-13.
- Hopp, H., and C.S. Slater. 1948. Influence of earthworms on soil productivity. Soil Sci. 66:421-428.
- Isensee, A.R., R.G. Nash, and C.S. Helling. 1990. Effect of conventional vs. no-tillage on pesticide leaching to shallow groundwater. J. Environ. Qual. 19:434–440.
- Joschko, M., W. Söchtig, and O. Larink. 1992. Functional relationship between earthworm burrows and soil water movement in column experiments. Soil Biol. Biochem. 24: 1545–1547.

- Juma, N.G. 1991. Interrelationships between soil structure, soil biota and primary plant production. Abstract #80 of International Workshop on Methods of Research on Soil Structure/Soil Biota Interrelationships. IAC, Wageningen.
- Kladivko, E.J., A.D. Mackay, and J.M. Bradford. 1986. Earthworms as a factor in the reduction of soil crusting. Soil Sci. Soc. Am. J. 50:191–196.
- Knight, D., P.W. Elliot, J.M. Anderson, and P. Scholefield. 1992. The role of earthworms in managed, permanent pastures in Devon, England. Soil Biol. Biochem. 24:1511–1517.
- Lavelle, P., and A. Martin. 1992. Small-scale and large-scale effects of endogeic earthworms on soil organic matter dynamics in soils of the humid tropics. Soil Biol. Biochem. 24:1491–1498.
- Lavelle, P., R. Schaefer, and Z. Zaidi. 1989. Soil ingestion and growth in *Millsonia anomala*, a tropical earthworm, as influenced by the quality of the organic matter ingested. Pedobiologia 33:379–388.
- Lee, K.E. 1985. Earthworms—Their Ecology and Relationships with Soils and Land Use. Academic Press, New York. 411 pp.
- Lee, K.E., and R.C. Foster. 1991. Soil fauna and soil structure. Aust. J. Soil Res. 29:745–775. Linden, D.R., and R.M. Dixon. 1976. Soil air pressure effects on route and rate of infiltration. Soil Sci. Soc. Am. J. 40:963–965.
- Logsdon, S.D., and D.R. Linden. 1992. Interactions of earthworms with soil physical conditions influencing plant growth. Soil Sci. 154:330–337.
- Mackay, A.D., and E.J. Kladivko. 1985. Earthworms and the rate of breakdown of soybean and maize residues in soil. Soil Biol. Biochem. 17:851–857.
- Marinissen, J.Y.C., and A.R. Dexter. 1990. Mechanisms of stabilization of earthworm casts and artificial casts. Biol. Fert. Soils 9:163–167.
- Martin, A. 1991. Short- and long-term effects of the endogeic earthworm *Millsonia anomala* (Omodeo) (Megascolecidae, Oligochaeta) of tropical savannas, on soil organic matter. Biol. Fert. Soils 11:234–238.
- Martin, A., and J.C.Y. Marinissen. 1993. Biological and physico-chemical processes in excrements of soil animals. Geoderma 56:331–347.
- McKeague, J.A., C.A. Fox, J.A. Stone, and R. Protz. 1987. Effects of cropping system on structure of Brookston clay loam in long-term experimental plots at Woodslee, Ontario. Can. J. Soil Sci. 67:571–584.
- Mouat, M.C.H., and R.G. Keogh. 1987. Absorption by soil of water-soluble phosphate from earthworm casts. Plant Soil 97:223–231.
- Oades, J.M. 1984. Soil organic matter and structural stability: Mechanisms and implications for management. Plant Soil 76:319–337.
- Oades, J.M. 1993. The role of biology in the formation, stabilization and degradation of soil structure. Geoderma 56:377–400.
- Owens, L.B., W.M. Edwards, and R.W. Van Keuren. 1984. Peak NO₃-N values in runoff from fertilized pastures. J. Environ. Qual. 13:310–312.
- Pawluk, S., and L. Bal. 1985. Micromorphology of selected mollic epipedons, pp. 63–83. In L.A. Douglas and M.L. Thompson (eds.). Soil Micromorphology and Soil Classification. SSSA Spec. Publ. 15. Soil Sci. Soc. Am., Madison, WI.
- Propes, K.L., F.W. Simmons, G.K. Sims, and C.W. Boast. 1993. Herbicide movement into and through earthworm induced soil macropores. North Central Weed Sci. Soc. Proc. 48:49–50.

- Satchell, J.E. 1967. Lumbricidae. pp. 259–322. In A. Burges and F. Raw (eds.). Soil Biology. Academic Press, London. 532 pp.
- Scharpenseel, H.W., and H. Gewehr. 1960. Studien zur Wasserbewegung im Boden mit Tritium-Wasser. Z. Pflanzenernährung u. Düngung 88:35–49.
- Schrader, S. 1991. Darstellung des Einflusses von Regenwürmern auf Redoxpotential und Ph-Wert mit Indicatoren. Mitt. Dtsch. Bodenkdl. Ges. 66:577–580.
- Schrader, S. 1993. Semi-automatic image analysis of earthworm activity in 2D soil sections. Geoderma 56:257–264.
- Sharpley, A.N., J.K. Syers, and J.A. Springett. 1979. Effect of surface-casting earthworms on the transport of phosphorus and nitrogen in surface runoff from pasture. Soil Biol. Biochem. 11:459–462.
- Shaw, C., and S. Pawluk. 1986. The development of soil structure by *Octolasion tyrtaeum*, *Aporrectodea turgida* and *Lumbricus terrestris* in parent materials belonging to different textural classes. Pedobiologia 29:327–339.
- Shipitalo, M.J., and R. Protz. 1988. Factors influencing the dispersibility of clay in worm casts. Soil Sci. Soc. Am. J. 52:764–769.
- Shipitalo, M.J., and R. Protz. 1989. Chemistry and micromorphology of aggregation in earthworm casts. Geoderma 45:357–374.
- Shipitalo, M.J., W.M. Edwards, W.A. Dick, and L.B. Owens. 1990. Initial storm effects on macropore transport of surface-applied chemicals in no-till soil. Soil Sci. Soc. Am. J. 54:1530-1536.
- Shipitalo, M.J., W.M. Edwards, and C.E. Redmond. 1994. Comparison of water movement and quality in earthworm burrows and pan lysimeters. J. Environ. Qual. 23:1345–1351.
- Shipitalo, M.J., R. Protz, and A.D. Tomlin. 1988. Effect of diet on the feeding and casting activity of *Lumbricus terrestris* and *L. rubellus* in laboratory culture. Soil Biol. Biochem. 20:233–237.
- Smettern, K.R.J. 1992. The relation of earthworms to soil hydraulic properties. Soil Biol. Biochem. 24:1539–1543.
- Smettem, K.R.J., and N. Collis-George. 1985a. Statistical characterization of soil biopores using a soil peel method. Geoderma 36:27–36.
- Smettem, K.R.J., and N. Collis-George. 1985b. The influence of cylindrical macropores on steady-state infiltration in a soil under pasture. J. Hydrol. 52:107–114.
- Smith, M.S., G.W. Thomas, R.E. White, and D. Ritonga. 1985. Transport of *Escherichia coli* through intact and disturbed soil columns. J. Environ. Qual. 14:87–91.
- Steenhuis, T.S., W. Staubitz, M.S. Andreini, J. Surface, T.L. Richard, R. Paulsen, N.B. Pickering, J.R. Hagerman, and L.D. Geohring. 1990. Preferential movement of pesticides and tracers in agricultural soils. J. Irrig. Drain. Eng. 116:50-66.
- Stehouwer, R.C., W.A. Dick, and S.J. Traina. 1993. Characteristics of earthworm burrow lining affecting atrazine sorption. J. Environ. Qual. 22:181–185.
- Stehouwer, R.C., W.A. Dick, and S.J. Traina. 1994. Sorption and retention of herbicides in vertically oriented earthworm and artificial burrows. J. Environ. Qual. 23:286–292.
- Stockdill, S.M.J. 1966. The effect of earthworms on pastures. Proc. N.Z. Ecol. Soc. 13: 68-75.
- Teotia, S.P., F.L. Duley, and T.M. McCalla. 1950. Effect of stubble mulching on number and activity of earthworms. Nebraska Agric. Exp. Sta. Bull. No. 165. 20 pp.

- Tisdall, J.M., and J.M. Oades. 1982. Organic matter and water stable aggregates in soils. J. Soil Sci. 33:141–163.
- Tomlin, A.D., M.J. Shipitalo, W.M. Edwards, and R. Protz. 1995. Earthworms and their influence on soil structure and infiltration. pp. 159–183. In P.F. Hendrix (ed.). Earthworm Ecology and Biogeography in North America. Lewis Publishers, Boca Raton, FL.
- Trojan, M.D., and D.R. Linden. 1992. Microrelief and rainfall effects on water and solute movement in earthworm burrows. Soil Sci. Soc. Am. J. 56:727-733.
- Turner, R.R., and K.F. Steele. 1988. Cadmium and manganese sorption by soil macropore linings and fillings. Soil Sci. 145:79–86.
- Tyler, D.D., and G.W. Thomas. 1981. Chloride movement in undisturbed soil columns. Soil Sci. Soc. Am. J. 45:459–461.
- Urbánek, J., and F. Dolezal. 1992. Review of some case studies on the abundance and on the hydraulic efficiency of earthworm channels in Czechoslovak soils, with reference to the subsurface pipe drainage. Soil Biol. Biochem. 24:1563–1571.
- Van Ommen, H.C., R. Dijksma, J.M.H. Hendrickx, L.W. Dekker, J. Hulshof, and M. Van den Heuvel. 1989. Experimental assessment of preferential flow paths in a field soil. J. Hydrol. 105:253–262.
- Van Veen, J.A., and P.J. Kuikman. 1990. Soil structural aspects of decomposition of organic matter by micro-organisms. Biogeochemistry 11:213–233.
- Watanabe, H., and S. Ruaysoongnern. 1984. Cast production by the Megascolecid earthworm *Pheretima* sp. in northeastern Thailand. Pedobiologia 26:37–44.
- White, R.E. 1985. The influence of macropores on the transport of dissolved and suspended matter through soil. Adv. Soil Sci. 3:95–120.
- Wildenschild, D., K.J. Jensen, K. Villholth, and T.J. Illangasekare. 1994. A laboratory analysis of the effect of macropores on solute transport. Ground Water 32:381–389.
- Zachmann, J.E., D.R. Linden, and C.E. Clapp. 1987. Macroporous infiltration and redistribution as affected by earthworms, tillage and residue. Soil Sci. Soc. Am. J. 51:1580–1586.